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Simone Maganuco*, Andrea Cau**
&
Giovanni Pasini***

First description of theropod remains from the Middle Jurassic (Bathonian) of Madagascar

Abstract - New theropod remains from the Middle Jurassic (Bathonian) of NW Madagascar are described that include 49 isolated teeth and a dorsal vertebra. Being referable to at least three taxa, they provide a first insight into the high morphological biodiversity in the Middle Jurassic theropods. They may represent the oldest Gondwanan material referable to the Abelisauridae and Coelurosauria found up to today; however, lacking more exhaustive data on theropod dentition, their affinities remain uncertain pending more complete material.

Key words: Madagascar, Middle Jurassic (Bathonian), Theropoda, vertebra, teeth.

Riassunto - Prima descrizione di resti di teropodi provenienti dal Giurassico medio (Bathoniano) del Madagascar.
Sono qui descritti per la prima volta resti di teropodi risalenti al Giurassico medio (Bathoniano) e provenienti dalle regioni nord-occidentali del Madagascar. Essi includono 49 denti isolati e una vertebra dorsale. Essendo ascrivibili ad almeno tre differenti taxa, questi resti offrono una prima importante testimonianza dell'elevata biodiversità dei teropodi del Giurassico medio. Essi inoltre rappresenterebbero a tutt'oggi i più antichi reperti gondwanani appartenenti ai taxa Abelisauridae e Coelurosauria, anche se, in assenza di materiale più completo e di ulteriori dati sulla dentatura dei teropodi, le loro relazioni filogenetiche restano incerte.

Parole chiave: Madagascar, Giurassico medio (Bathoniano), Theropoda, vertebra, denti.

Introduction

The Mesozoic Gondwanan theropod record has improved considerably over the last twenty years, thanks to recent efforts in South America, Indo-Pakistan, Africa, Madagascar and Antarctica.

However, most of - if not all - the new discoveries were limited to Cretaceous

*Museo Civico di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy, e-mail: simonemaganuco@iol.it (corresponding author).
**Via Fontana 6, 43029 Traversetolo (Parma), Italy, e-mail: avialae@yahoo.it
***Museo Civico dei Fossili di Besano, Via Prestini 5, 21050 Besano (Varese), Italy, e-mail: museodibesano@tiscali.it

rocks, while the record of Jurassic theropod from terrestrial deposits continues to be extremely poor. Jurassic remains from several Gondwanan localities include a small number of theropods, among which: the Italian specimen MSNM V3664 from the Early Jurassic (Sinemurian) of Saltrio (Dal Sasso, 2003); the fragmentary Indian theropod *Dandakosaurus* described by Yadagiri (1982); *Ozraptor* from the Aalenian of Australia (Long & Molnar, 1998); the basal theropod *Cryolophosaurus* from the Pliensbachian of Antarctica (Hammer & Hickerson, 1994); the tetanurans *Piatnitzkysaurus* (Bonaparte, 1979) and *Condorraptor* (Rauhut, 2005a) from the Callovian of South America; the well known coelophysid *Megapnosaurus* (previously known as *Syntarsus* [Raath, 1969]), from the Early Jurassic of Zimbabwe; the Middle Jurassic Moroccan taxon *Megalosaurus mersensis*, now regarded as a nomen dubium (Allain, 2002); some remains referred to tetanuran and ceratosaurian theropods and the skeleton of the neoceratosaur *Elaphrosaurus* from a single Late Jurassic locality in Tanzania (Janensh, 1920, 1925; Rauhut, 2005b); and the peculiar fossil teeth from the Late Jurassic/ Early Cretaceous boundary of Ethiopia referable to the allosauroid *Acrocanthosaurus* and to a dromaeosaur-like theropod (Goodwin *et al*., 1999). In Madagascar some isolated teeth (Besairie, 1936; Lavocat, 1955; Flynn *et al*., 1997) and two presacral vertebrae (Flynn *et al*., 1997) have been reported, but all descriptions by those authors are so scarce that do not allow precise diagnosis and any comparison. Here we describe new theropod material, including a fragmentary vertebra and 49 isolated teeth, from the Bathonian of Madagascar. Being referable to at least three suprageneric theropod taxa, the new specimens represent a sample of the high diversity present in the Malagasy Middle Jurassic ecosystem. Perhaps including the oldest Gondwanan material referable to the Abelisauridae and Coelurosauria, they also suggest new scenarios about the still poorly known paleogeographic and evolutionary context of those taxa.

Geological context

All the material here figured and described comes from the Middle Jurassic strata of the Mahajanga Basin (north Madagascar) (Figs. 1, 2). The specimens have been found at the ground surface, eroded, transported and concentrated in small areas during the raining seasons. For this reason, the possibility that fossil materials may have been reworked has been taken into consideration. Despite the lacking of more specific stratigraphic data, the general features of such well exposed, subhorizontal continental deposits, locally containing heteropies with transgressive-marine sediments, as evidenced by petrographic features and faunal assemblages, allow us to state that the material pertains without doubt to a single Subunit referable to the Isalo IIIb "faciés mixte - dinosauriens" Bathonian, *sensu* Besairie (1972) (Fig. 3). This is confirmed by the results of the analysis of the matrix filling the neural canal of the specimen MSNM V5804. The composition of the matrix of such sample is a fine-grained sandstone with carbonatic cement; the sediment is well sorted and it is mainly composed by quartz grains (grain-size in the range 0.2 - 1 mm), with accessory zircon and garnet, with rare ilmenite. The sedimentologic features confirm a non-marine deposition environment but, very likely, a fluviallacustrine basin, with possible brackish facies. Such stratigraphic data seem to correspond to those reported by Besairie (1972), for the description of the continental Bathonian and the "faciés mixte" Isalo IIIb of "Route de Majunga". For this reason we can date our samples as Bathonian (ICS stage), 167.7 – 164.7 MA (Gradstein *et al.*, 2004).

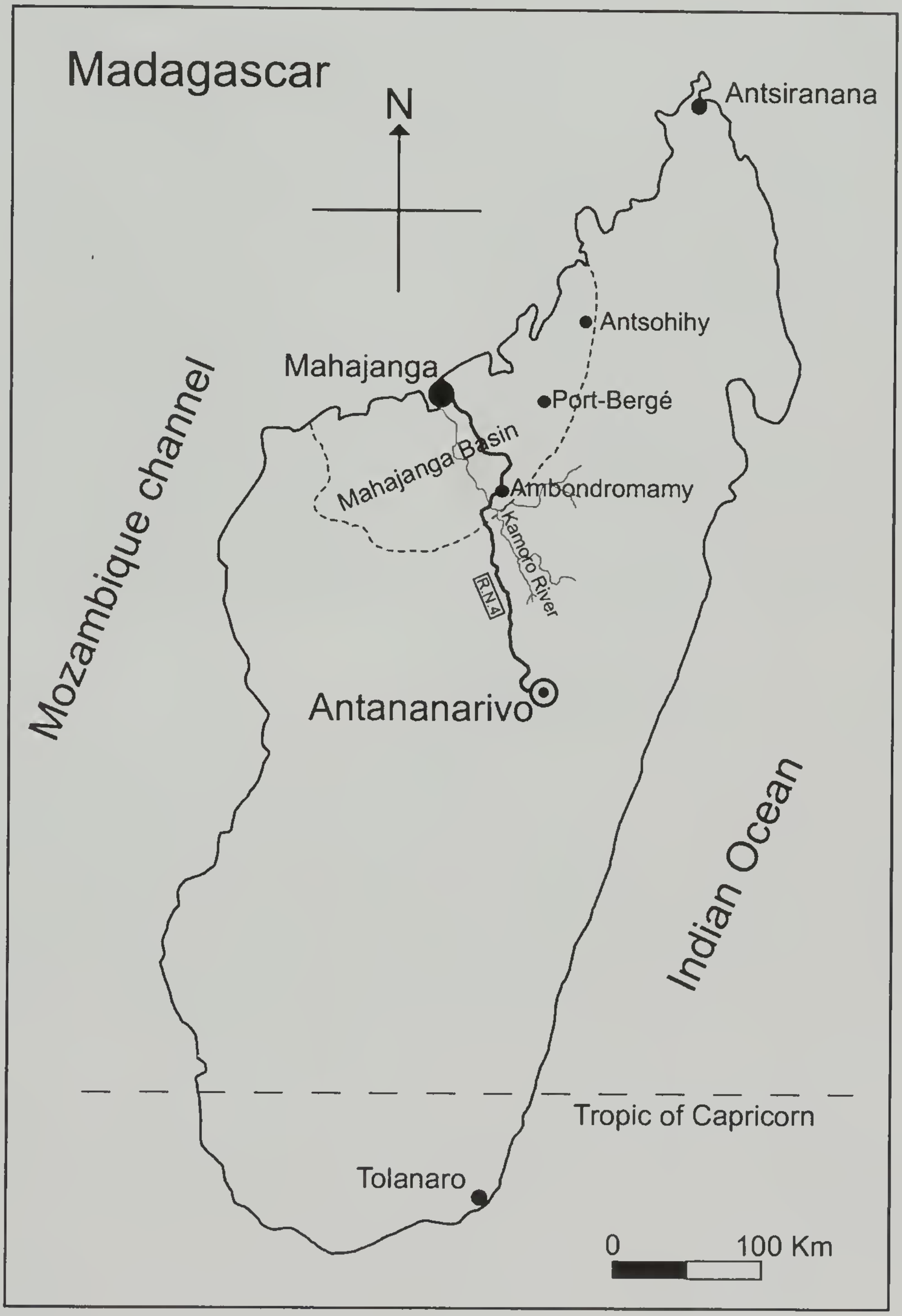

Fig. 1 - Geographic map of Madagascar in which are highlighted the main localities and landscape elements cited into the text.

Fig. 1 - Mappa geografica del Madagascar nella quale sono evidenziati le principali località e gli elementi del paesaggio citati nel testo.

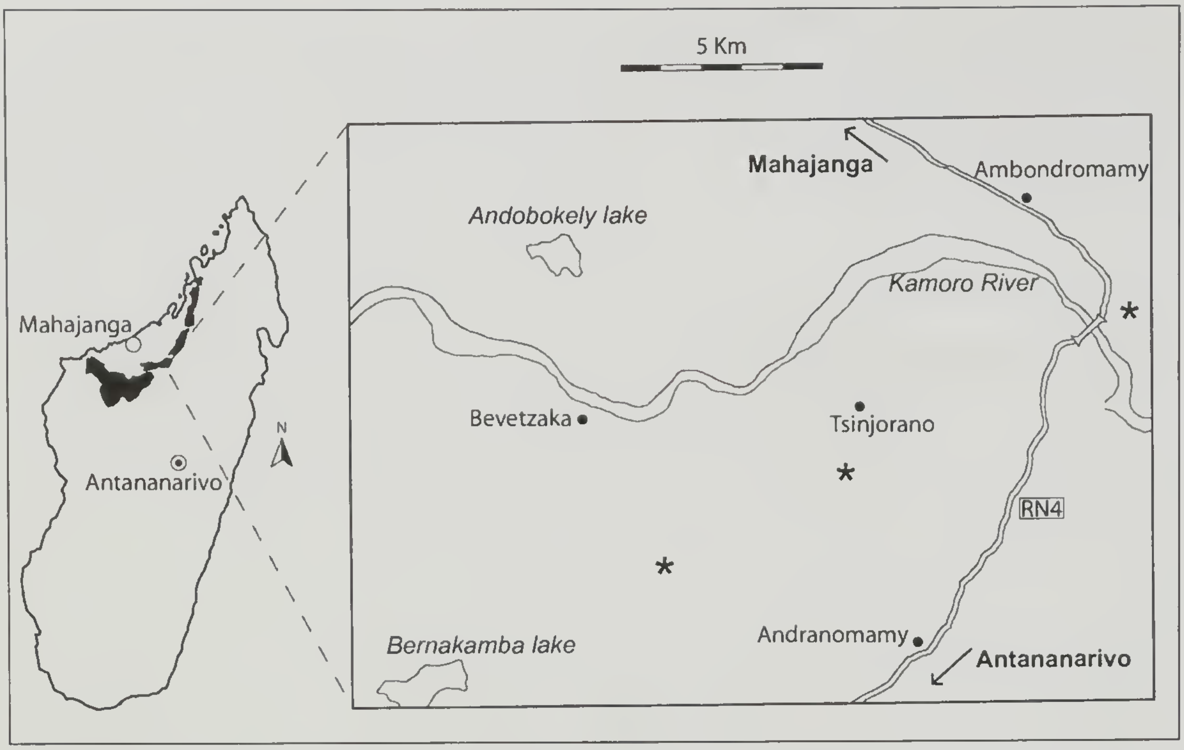

Fig. 2 - Geological map of the Triassic and Jurassic outcrops of the Mahajanga Basin (black areas on the left) and close-up of the localities recently prospected by one of the authors (G. Pasini). Some of the material here described comes from the sites marked by the asterisks (see the text).
Fig. 2 - Mappa geologica degli affioramenti triassici e giurassici del Bacino di Mahajanga (aree annerite nella cartina a sinistra) e particolare delle località recentemente prospettate da uno degli autori (G: Pasini). Parte del materiale qui descritto proviene dai siti contrassegnati dagli asterischi (vedere il testo).

Material location and history

As mentioned above, the material includes a fragmentary vertebra and 49 isolated teeth housed in the Collection of Fossil Vertebrates of the Museo Civico di Storia Naturale di Milano (acronym MSNM V). Specimens MSNM V5778 - 5798, V5805-5818, and V5820-5824 have been found in loose sediments on the surface by G. Pasini with the help of local prospectors during a first prospection in 2001. In particular, specimens V5805 and 5806 come from the neighbouring of Ambondromamy (Figs. 1, 4); MSNM V5778 - 5798, and 5820 come from an area between Ambondromamy and Port Bergè (Fig. 1); specimens MSNM V5807-5818, and V5821-5824 have been found at north of Port-Bergé (Fig. 1). The remaining part of the material has been collected on the surface too by G. Pasini in April 2003 (see Fig. 2), during the prospections made in the Museo Civico dei Fossili di Besano and Museo Civico di Storia Naturale di Milano joint expedition: the specimen MSNM V5819 has been found between Tsinjorano and the bridge on the Kamoro River (Fig. 5); the specimen V5804 has been found near the same bridge along the weathered sides of a low tanety (local name for "hill") on the right bank of the Kamoro River; MSNM V5799, 5800, and 5956-5962 come from an area near Tsinjorano, south-west to Ambondromamy. Prospecting activity in the latter area (concession to prospection acquired from Bureau du Cadastre Minier n. 3402-3405/Carte 41) has yielded additional vertebrate remains already published (pterosaur teeth [Dal Sasso & Pasini, 2003]), to be published (large archosaur remains [Maganuco *et al.*, submitted]) or still uncatalogued (one crocodilian osteoderm, few crocodilian teeth, several sauropodomorph teeth, and few sauropodomorph bones [mostly phalanges including some unguals]).

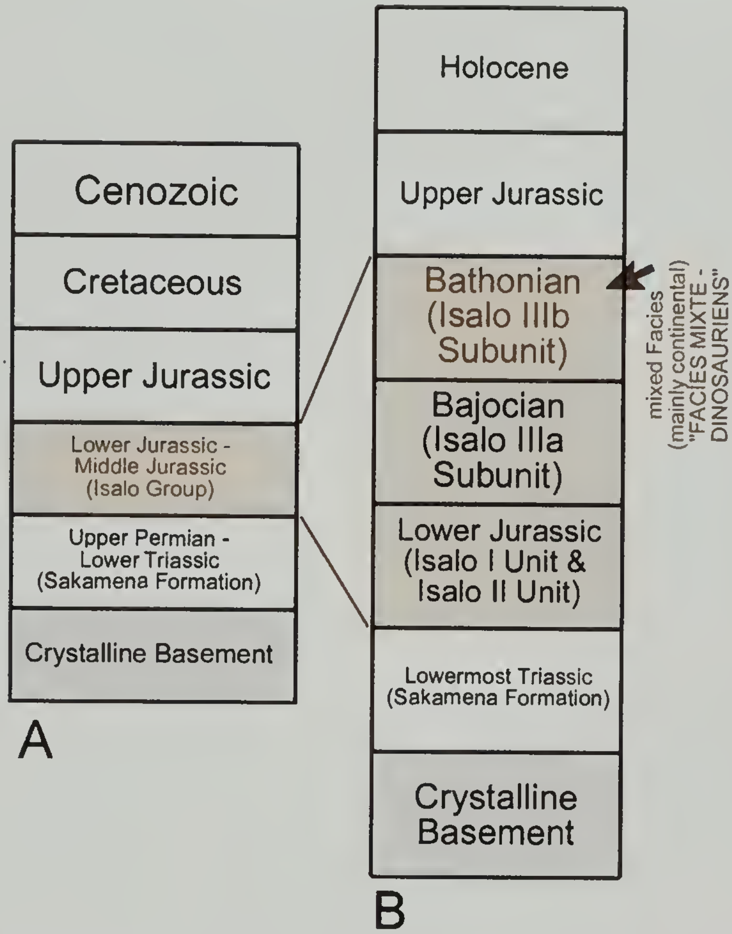

Fig. 3 - Schematic geological sections of the whole Mahajanga basin (A) and near the village of Ambondromamy (B). The arrow indicates the Isalo IIIb Subunit "Faciés mixte - dinosauriens" Bathonian *sensu* Besairie (1972), which our specimens come from. Modified from Besairie (1972).
Fig. 3 - Sezione geologica schematica generale del bacino di Mahajanga (A) e in particolare nei pressi di Ambondromamy (B). La freccia indica la Subunità Isalo IIIb "Faciés mixte - dinosauriens" Bathonian *sensu* Besairie (1972), dalla quale provengono gli esemplari. Tratta da Besairie (1972), semplificata.

Methods

The specimens are pictured in digital photographs (Nikon Coolpix 995). Some preparation was done only on the vertebra (specimen MSNM V5804), in order to remove matrix from the neural canal. Analysis of this matrix was made by S.E.M.. Measurements were taken with a digital calliper; cross-sections of the teeth were obtained by casting them with silicon RTV rubber and cutting of their plaster replicas. The cross-section drawings were made under camera lucida. In describing the teeth we have utilized the following terms defined by previous authors: TCH = tooth crown height; FABL = fore-aft basal length; BW = basal width; BCR (FABL/BW) = basal compression ratio; ER (FABL/TCH) = elongation ratio (all these terms are from

Currie *et al.* [1990], Farlow *et al.* [1991], and Sankey *et al.*, [2002]); DSDI = denticle size difference index (Rauhut & Werner, 1995; Rauhut, 2002). The material has been subdivided into different morphotypes on the basis of several features including: general morphology of both the crown and the carinae, cross sections, BCR, ER, development of the mesial carina, shape and orientation of the denticles, DSDI, development of the blood grooves. We have opted to measure denticles per 3 mm because in some cases the teeth do not have denticles over a 5 mm length, whereas denticles per 1 mm made us difficult to obtain integers. The denticle count, where possible, was taken at mid crown height because in some of the specimens the size of the denticles decreases at the apical and basal ends of the carinae (Chandler, 1990; Sweetman, 2004). The number of denticles per mm has been evaluated also taking into consideration the TCH, because according to several authors (Farlow *et al.*, 1991; Rauhut & Werner, 1995; Charig & Milner, 1997) denticle size usually scales to tooth size. For example, V5819 and V5792, two teeth belonging to different morphotypes, have the same number of denticles per mm even if the TCH of the former is more than twice the one of the latter. According to Rauhut & Werner (1995) and Rauhut (2002) the DSDI was used as a size independent criterion of comparing theropod teeth. The systematic significance of this parameter, however, must be evaluated in combining it with the other features of the teeth, because its variation range may be the same for many theropod taxa and may be influenced by individual or ontogenetic variability (Farlow *et al.*, 1991). For example, Carr & Williamson (2004) reported that in some tyrannosaur specimens the DSDI among dentary teeth is higher than in the maxillary teeth, whereas in juvenile tyrannosaurids (Currie & Dong, 2001; Carr & Williamson, 2004) and at least in some juvenile abelisaurids (Fanti, pers. comm. 2004) the DSDI is significantly higher than in the adults. The total range of the ERs resulted only partially useful to characterize the morphotypes because they overlapped each other. This is partly due to the fact that ER is influenced also by individual variation, as it was reported by Currie *et al.* (1990) for *Dromaeosaurus*, in which teeth with relatively high and low elongation ratio pertain respectively to upper and lower jaws. Nevertheless, the mean values of the ER have faintly indicated some trends among the different morphotypes. According to previous authors (Stromer, 1934; Colbert, 1989; Rowe, 1989; Zinke, 1998; Xu & Wu, 2001; Carrano *et al.*, 2002; Rauhut, 2004), the BCR, and both presence and development of the mesial carina vary along the tooth row. In general, in going toward the rear of the tooth row the teeth tend to become more labiolingually flattened and the mesial carina tends to become longer and serrated. Some differences can be found also between the upper and the lower jaws, as, for example, in the ceratosaurid *Genyodectes* which have maxillary teeth more labioligually flattened than the dentary teeth (Rauhut, 2004). Therefore the BCR and the features of the mesial carina were useful, other than to subdivide the specimens into different morphotypes, also to recognize when two morphotypes differ each other only for features reflecting different position into the jaws. Finally, Currie and Candeiro (Candeiro *et al.*, 2004) pointed out that tooth cross-sections are unique to theropod families. It is not the aim of this paper to evaluate if cross section at the base alone is diagnostic at family-level, nevertheless we recognized in that feature a certain degree of systematic significance. All the systematic terms are used following Padian *et al.* (1999).

Fig. 4 - One of the outcrops of the Middle Jurassic (Bathonian) Isalo IIIb subunit near the village of Ambondromamy (photo G. Pasini).
Fig. 4 - Uno degli affioramenti della subunità stratigrafica Isalo IIIb, riferibile al Giurassico medio (Bathoniano), nei pressi del villaggio di Ambondromamy (foto G. Pasini).

Fig. 5 - The bridge on the Kamoro River in the neighbouring of which the specimens MSNM V5804 has been found (photo G. Pasini).
Fig. 5 - Il ponte sul fiume Kamoro, nelle vicinanze del quale è stato trovato l'esemplare MSNM V5804 (foto G. Pasini).

SYSTEMATIC PALEONTOLOGY
DINOSAURIA Owen, 1841
THEROPODA Marsh, 1881
Gen. et spec. indet.

Vertebra (Fig. 6; Tabs. 1, 2)

Description. The specimen MSNM V5804 consists of an isolated vertebra in which the centrum and the base of the neural arch are preserved. The amphicoelus centrum is almost complete and elongated rostrocaudally, lacking only some lateral margin of the articular faces. Judging to the shape of their preserved margins, we suppose that both the rostral and caudal faces were taller than wide (Fig. 6A, C). The body of the centrum lacks pneumatic foramina and there are not traces of either a ventral sulcus or carina on its ventral surface. The middle region of the centrum is strongly compressed mediolaterally and has a smooth surface, whereas the expanded rostral and caudal portions bear shallow sub-horizontal grooves (Fig. 6D). In lateral view (Fig. 6B), the curvature of the ventral surface is quite marked and the neurocentral suture is clearly visible. By analogy with crocodilians (Brochu, 1996) the absence of suture closure could indicate that the individual was not either fully mature or fully grown at death. Only a little basal portion of the neural arch is preserved, lacking most of the zygapophyseal regions and the neural spine. However, in lateral view, remains of both parapophysis and prezygapophysis can be seen on the right side (Fig. 6B). The parapophysis is fully migrated onto the neural arch. Due to the fracture, the transverse processes (diapophy-

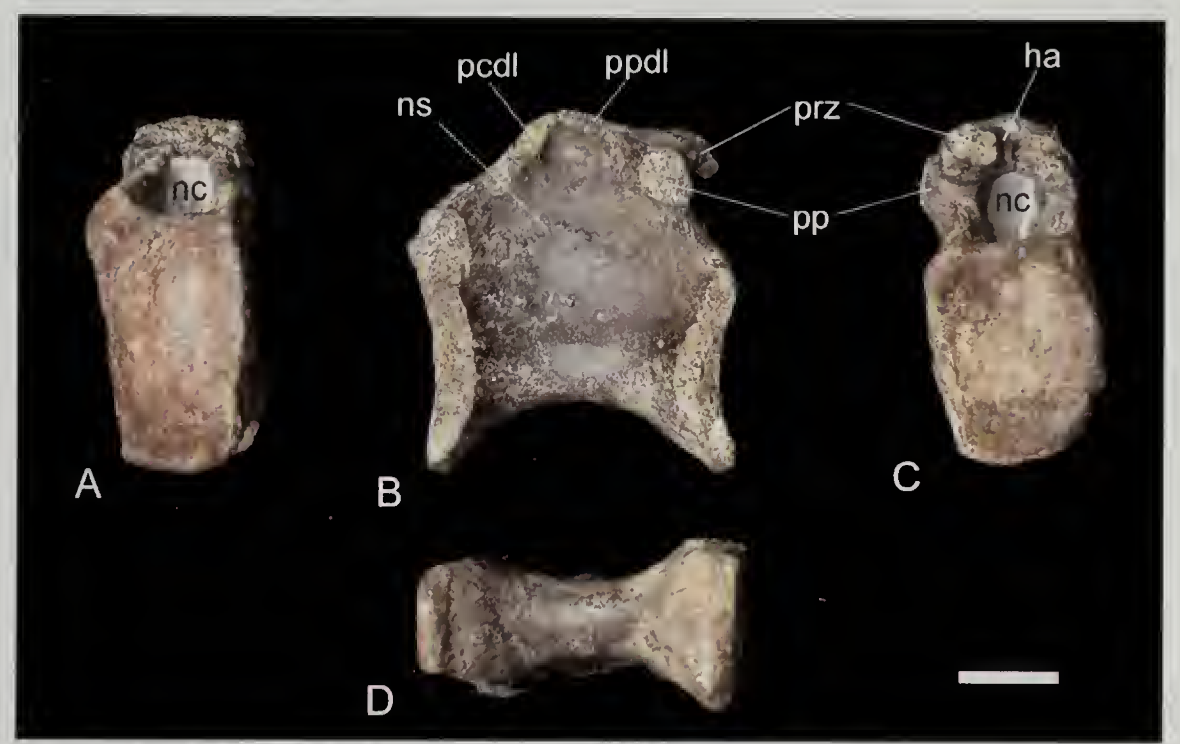

Fig. 6 - Specimen MSNM V5804 in caudal (A), right lateral (B), rostral (C), and ventral (D) views. Abbreviations: ha, hypantrum; nc, neural canal; ns, neurocentral suture; pcdl, posterior centrodiapophyseal lamina; pp, parapophysis; ppdl, paradiapophyseal lamina; prz, prezygapophysis. Scale bar equals 2 cm.
Fig. 6 - Specimen MSNM V5804 nelle viste caudale (A), laterale destra (B), rostrale (C) e ventrale (D). Abbreviazioni: ha, ipantro; nc, canale neurale; ns, sutura neurocentrale; pcdl, lamina centrodiapofisale posteriore; pp, parapofisi; ppdl, lamina paradiapofisale; prz, prezigapofisi. La scala metrica equivale a 2 cm.

ses) and the postzygapophyses are not preserved. The medioventral corners of the prezygapophyses abut one another above the neural canal enclosing a dorsoventrally oriented notch. The lack of traces of the transverse processes on the preserved part of the neural arch strongly suggests that the arch was high and borne caudo-dorsally inclined transverse processes. The base of the neural arch contributes to the dorsal margin of the caudal articular surface of the centrum. The almost rounded pleurocentral depression present on each side of the neural arch (similar to the middle chonos of *Dilophosaurus* described by Welles [1984]) is bordered dorsally by a continuous ridge-like process that we interpret as remains of the paradiapophyseal and posterior centrodiapophyseal laminae (Fig. 6B) (Wilson, 1999).

Tab. 1 - Basic measurements of the vertebra (specimen MSNM V5804) described in the text. Measurements are in mm.
Tab. 1 - Misure principali della vertebra (esemplare MSNM V5804) descritta nel testo. Le misure sono in mm.

Ventral side:	rostrocaudal length	55.4 mm
	minimum mediolateral width	11.8 mm
Rostral face:	dorsoventral length	40.4 mm
	mediolateral length	31.9 mm (as preserved); about 35 mm (hypothesized)
Caudal face:	dorsoventral length	41.9 mm
	mediolateral length	25.4 mm (as preserved); about 35 mm (hypothesized)
Neural canal:	rostral face dorsoventral length	12.7 mm
	rostral face mediolateral length	8.5 mm
	caudal face dorsoventral length	10.5 mm
	caudal face mediolateral length	9.1 mm

Discussion. The vertebra is here considered a caudal dorsal on the basis of several features including parapophysis fully migrated onto the neural arch and subcircular outline of the ventral surface; also the inferred position of the transverse processes is consistent with the typical condition in medium or caudal dorsals. The small subhorizontal grooves on the centrum surface do not represent a diagnostic feature, being present in theropods, but also in crocodiles, and some ornithopods. The presence of paradiapophyseal and posterior centrodiapophyseal laminae may indicate that MSNM V5804 belongs to a saurischian dinosaur. The presence of laminae at the level of the neurocentral suture is also known in the basal dinosauromorph *Silesaurus* (Dzik, 2003) and in some rauisuchians, while the laminae are weakly developed in ornitischians and in the greatest part of other not-saurischian archosaurs (Wilson, 1999). The dorsoventrally oriented notch enclosed by the prezygapophyses (Fig. 6C) is here interpreted as the hypantrum (Ostrom, 1969): this accessory vertebral articulation is a saurischian feature (Sereno, 1999; Rauhut, 2003) absent only in few derived lineages of sauropods and coelurosaurians (Wilson, 2002; Forster *et al.*, 1998) and convergently developed in many lepidosaurian clades (Romer, 1956). In combining the above mentioned features, we refer MSNM V5804 to Saurischia. Although sauropodomorph phylogeny is strongly based on vertebral morphology, the fragmentary nature of MSNM V5804 prevents us from recognizing any diagnosable sauropodomorph feature. By the way, the narrow and long centrum is quite typical to basal Theropoda and the general shape of the specimen closely resembles that of some members of this clade. In particular, in MSNM V5804 the ratio between centrum length and rostral face height is > 4/3, resembling that of *Elaphrosaurus* (Janesh, 1925), *Eustreptospondylus* (Walker, 1964), *Liliensternus* (Huene, 1934), Ornithomimosauria (Osmolska *et al.*, 1972), Alvarezsauridae (Perle *et al.*, 1994), *Streptospondylus* (Allain, 2001.), *Masiakasaurus* (Sampson *et al.*, 2001), *Dilophosaurus* (Welles, 1984), and differing from *Szechuanosaurus zigongensis* (Gao, 1998), *Condorraptor currumili* (Rauhut, 2005a), allosauroids (Currie & Zhao, 1993), tyrannosaurids (Brochu, 2003), *Baryonyx* (Charig & Milner, 1997), *Torvosaurus* (Britt, 1991), *Ceratosaurus* (Gilmore, 1920), and *Carnotaurus* (Bonaparte *et al.*, 1990) which share the opposite condition (rostro-caudal length of the centrum < 4/3 of the rostral facet heigth of the centrum), and from coelophysids, in which dorsal centra are apomorphically more elongated (Colbert, 1989). In accepting the caudal dorsal nature of the vertebra, the absence of ventral sulcus or carina cannot be considered a diagnostic feature. However, MSNM V5804 shows a combination of plesiomorphic features for Theropoda (see also Tab. 2) that are useful to exclude its belonging to some taxa:

- pneumatization of the centrum absent: lack of pneumatic foramina is a theropod symplesiomorphy lost in some lineages such as *Acrocanthosaurus* (Harris, 1998), *Carnotaurus*, Tyrannosauridae, *Torvosaurus* and advanced Oviraptorosauria (Makovicky & Sues, 1998);
- rostral articular facet is an ellipse with major axis dorsoventrally oriented: this character is shared with most theropods with the exception of some abelisauroids (Coria & Salgado, 2000) and oviraptorosaurians (Makovicky & Sues, 1998), in which the rostral facet is wider than high;
- neural canal height about 1/3 the height of the rostral face: MSNM V5804 differs from *Aviminus* (Kurzanov, 1981), Alvarezsauridae, and Aves (pers. obs.) in which the height of the neural canal is more than 2/5 the height of the rostral face;
- dorsal centrum cylindrical, with the central section thickness greater than 3/5 of the height of the cranial face: MSNM V5804 differs from most allosauroids in which the vertebral bodies are hourglass shaped, with their central section thickness less than 3/5 of the height of the cranial face (Holtz, 2000);
- prezygapophyses abut one another above the neural canal: as in non-maniraptoran theropods, the prezygapophyses of MSNM V5804 abut one another above the neural canal, whereas in maniraptorans (Makovicky & Sues, 1998) zygapohyses are placed laterally to the neural canal and are separated by a groove for interspinuous ligaments.

In conclusion, on the basis of both the negative evidences discussed above and the presence of theropod plesiomorphies, MSNM V5804 cannot be included in any of the following derived theropod groups: Abelisauroidea, Allosauroidea, Tyrannosauridae, Maniraptora and Coelophysidae. Moreover, we can also infer that there is a certain degree of resemblance between MSNM V5804 and the dorsal vertebrae of *Elaphrosaurus*, *Eustreptospondylus*, *Streptospondylus* and *Dilophosaurus*: MSNM V5804 could represent a basal member of one of the stems of these taxa, but additional material is needed to make a precise phylogenetic assignment. For this reason, we refer MSNM V5804 to Theropoda incertae sedis.

Tab. 2 - Comparison between the specimen MSNM V5804 and some other theropod dorsal vertebrae.
Tab. 2 - Confronto tra l'esemplare MSNM V5804 e alcune vertebre dorsali di altri teropodi.

Taxon	Shape of the rostral face	Anterocaudal centrum length / rostral face height	Lamination at the centrum - neural arch boundary	Pneumatic foramina in centrum: a) absent; b) present	Neural canal height / rostral face height	Position of the prezygapophyseal medioventral corner: a) at the level of the neural canal border; b) above the neural canal; c) beyond the lateral border of the neural canal	Type of parapophysis: a) simple tubercle; b) robust and proximodistally expanded
Baryonyx walkeri (Charig & Milner, 1997)	subcircular	1.3 - 1.4 times	robust	a	less than 0.25	a	a
Carnotaurus sastrei (Bonaparte *et al.*, 1990)	wider than tall	subequal	robust	b	less than 0.25	b	b
Ceratosaurus magnicornis (Madsen & Welles, 2000)	subcircular	subequal	robust	a	less than 0.3	b	b
Coelophysis bauri (Colbert, 1989)	subcircular	more than 2 times	weak	a	0.35 - 0.45	a	a
Dilophosaurus wetherilli (Welles, 1984)	taller than wide	1.3 - 1.4 times	weak	a	0.35 - 0.45	a	b
Ilokelesia aguadagrandensis (Coria & Salgado, 2000)	wider than tall	1.3 - 1.4 times	weak	a	0.35 - 0.45	a	b
Masiakasaurus knopfleri (Carrano *et al.*, 2002)	subcircular	1.5 - 2 times	weak	a	?0.35 - ?0.45	b	?
Microvenator celer (Makovicky & Sues, 1998)	wider than tall	1.5 times	weak	b	0.25 - 0.35	c	a
Silesaurus opolensis (Dzik, 2003)	taller than wide	1.3 - 1.4 times	weak	a	0.35 - 0.45	c	b
Sinraptor dongi (Currie & Zhao, 1993)	taller than wide	subequal	robust	a	less than 0.25	b	a
MSNM V5804	taller than wide	1.3 - 1.4	weak	a	0.25 - 0.35	b	a

Isolated teeth (Figs. 7-11; Tabs. 3-4)

All the teeth can be considered true ziphodont *sensu* Prasad & de Lapparent de Broin (2002), in having clearly individualized denticles on the carinae, which are not the result of prolongation of the enamel ridges of the crown. Actually, on the basis of the published material available to the present authors it was not possible to find exhaustive and well comparable tooth data for many theropod and ziphodont crocodylomorph taxa and thereby to establish some precise criteria for demonstrating definitely their belonging. Nevertheless we have compared our material with several crocodylomorph specimens beautifully figured by Prasad & de Lapparent de Broin (2002), baurusuchian teeth (Riff, pers. com. 2005), some teeth of *Majangasuchus* present in the MSNM collection (in study by Fanti), and the teeth of *Hamadasuchus* figured by Larsson & Sidor (1999). Despite of the fact that ziphodont crocodiles exhibit a wide range of tooth morphology with variation in surface ornamentation, serrations, and cross sectional outline (see Prasad & de Lapparent de Broin [2002]), the Malagasy material here described does not show significant affinities with the material belonging to those taxa. Rather, the combination of the features mentioned in the Methods section allow us to recognize eight different morphotypes with theropod affinities. Only the specimen MSNM V5960, which consists of a poorly preserved tip of the crown with denticles eroded till their base, can not be included in any of the morphotypes, and also its belonging to the Theropoda can be only tentatively hypothesized. The morphotype 2 includes roughly the 40% of the specimens, whereas the morphotypes 7 and 8 include respectively one and two teeth. However, the relatively small number of specimens and the fact that they were collected during prospection activity do not allow us to make statements about abundance of the taxa. As briefly mentioned in the Methods section, it is also verisimilar that some of the morphotypes belong to the same taxon, their features reflecting different positions in the jaw. Nevertheless, even taking into account several factors of variability and the fact that in some theropods there is a certain degree of heterodonty (Currie *et al.*, 1990), the Malagasy morphotypes here described should pertain to not less than 3, maybe 5, different supra-generic taxa. Disrespecting to their belonging to different morphotypes, the Malagasy specimens here studied share the following features: the pulp cavities are clearly visible and filled with matrix; wear is present on the labial and lingual sides of the crown near the tip (where it is preserved); where the apical portion of the root is preserved too, a constriction between the crown and the root is never present; where the mesial carina is present, the denticles wrap around the tip of the tooth onto the distal carina (as pointed out by Currie & Carpenter [2000], this is a common feature among theropods, therefore has limited taxonomic utility). The eight morphotypes are the following:

Morphotype 1 (Fig. 7)

Referred specimens: MSNM V5778 (Fig. 7A-H), V5807 (Fig. 7I), V5820.

Description. Those specimens can be easily recognized as rostral teeth due to their peculiar shape, position of the carinae and cross-sections. Both the ERs and the BCRs are quite low, as expected in rostral teeth, and one of the specimens (V5820) is nearly sub-circular in cross section. The distal margin of the crown is nearly straight or gently convex in labial and lingual views, with the convexity that is more pronounced in the mid of the margin (Fig. 7A, C). The labial surface is strongly convex and smooth, and becomes flat or slightly concave near the bases of the carinae. The lingual surface is convex in its mid part, then becomes flat till the proximity of the carinae in which is markedly concave. In cross sections, V5778 is slightly asymmetrical respect its labiolingual axis, with the mesial carina placed on the lingual side (Fig. 7G, H). The asymmetry increases in V5807 and is maximal in V5820, in which the mesial carina projects nearly perpendicular to the lingual side. Judging from these features, we can argue that, among our three specimens, V5820 occupied the rostralmost position, whereas V5778 the caudalmost one. The apical portion of the mesial carina is missing in both V5778 and V5820, but there are no doubts that the carinae met apically and run along the entire height of the crown, as can be seen in V5807. In mesial view (Fig. 7D), the mesial carina is gently S-shaped (convex toward the lingual side in the basal half and convex toward the labial side in the apical half). In distal view (Fig. 7B), the distal carina is only just concave lingually, following the faint curvature of the crown. Both the carinae are serrated, with the denticles slightly inclined toward the tip of the crown. The distal denticles (Fig. 7E, I), roughly three times longer than wider, are preserved in all the specimens, but their tips, pointed and oriented toward the apex of the tooth crown, can be seen only in V5807 (Fig. 7I) and, in a low number of denticles, in V5820. The mesial denticles, nearly equal to the distal ones in base length (DSDI = 1.00), are not well preserved with the exception of those of V5778 (Fig. 7F), in which only the tips are missing. In that specimen the mesial denticles appear quite tall, only slightly shorter than the distal ones. The enamel is well preserved in V5778 and V5807, and in the latter it bears shallow curved impressions with the concavity turned toward the tip of the crown. The blood grooves are well visible even without using a microscope or a lens, and inclined toward the base of the crown.

Comparisons. In accepting their rostral position, we can observe that the teeth belonging to this morphotype are markedly different from the typical U-shaped premaxillary teeth of the tyrannosauroids (Holtz, 2001; Hutt *et al.*, 2001). In labial and lingual views and in cross sections, they superficially resemble the premaxillary tooth of *Dromaeosaurus* figured by Currie *et al.* (1990: fig. 8.6D) but size, shape, and orientation of both the denticles and the blood grooves are markedly different. They resemble also *Acrocanthosaurus*, allosaurids and dromeosaurids, but not *Torvosaurus* (Currie & Carpenter, 2000), in having the mesial carina that is placed on the midline of the crown at the tip and then twists lingually. Again, size, shape, and orientation of the denticles and the blood grooves in those taxa are decidedly different, particularly in *Acrocanthosaurus* (Currie & Carpenter, 2000) in which, despite the great size of the crown, the denticles are slightly smaller than those of the teeth of the morphotype one. Some resemblances have been found with some teeth of the Neoceratosauria, but not with the ceratosaurids (*sensu* Rauhut, 2004) nor the noasaurid *Masiakasaurus*. The ceratosaurid *Genyodectes* has premaxillary teeth in which the distal carina is displaced labially (Rauhut, 2004) whereas Currie & Carpenter (2000) reported that *Ceratosaurus* has no mesial carina on the premaxillary teeth. The teeth of the noasaurid *Masiakasaurus*

(Sampson *et al.*, 2001) are completely different, being spatulate and strongly recurved, and having striations on the distal surface, rounded apex of the crown, and carinae that bear faint serrations and are displaced on labial and lingual sides (Carrano *et al.* 2002). The rostral teeth of the abelisaurids have not been described up to today. However, we have had the opportunity to make some comparisons with some abelisaurid teeth referred to *Majungatholus atopus* collected by the MSNM in the Cretaceous rocks of the Mahajanga basin. Those Late Cretaceous Malagasy specimens, housed in the collection of the MSNM and at present in study by Fanti (pers. com. 2005), closely resemble the teeth of the morphotype 1, being only slightly different in the shape and in having a lower number of denticles per mm on both the carinae in teeth of comparable TCH. Finally, the morphotype 1 resembles very much the lateral teeth belonging to the morphotypes 2 and 3 in both denticle morphology and aspect of the blood grooves.

Fig. 7 - Morphotype 1. Specimen MSNM V5778: labial (A), mesial (B), lingual (C), and distal (D) views, close-ups of the distal (E) and mesial (F) denticles, and cross sections at the base (G) and mid height (H) of the crown. Specimen MSNM V5807: close-up of the distal (I) denticles. Abbreviations: d, distal carina; li, lingual side. Scale bar equals 5 mm.
Fig. 7 - Morfotipo 1. Esemplare MSNM V5778: viste labiale (A), mesiale (B), linguale (C) e distale (D), particolari dei denticoli distali (E) e mesiali (F), e sezioni trasverse alla base (G) e a metà altezza (H) della corona. Esemplare MSNM V5807: particolare dei denticoli distali (I). Abbreviazioni: d, carena distale; li, lato linguale. La scala metrica equivale a 5 mm.

Morphotype 2 (Fig. 8A-E)

Referred specimens: MSNM V5780, V5781, V5782, V5783, V5784, V5788, V5790, V5794, V5798, V5799 (Fig. 8A-E), V5806,V5808, V5810, V5814, V5817, V5818, V5821, V5957, V5962.

Description. This morphotype includes 19 lateral teeth, characterized by having the crowns quite short and rather labiolingually compressed. This can be clearly seen looking at the mean values of the BCR and ER (Tab. 4) that represent respectively the lowermost and the highest among our morphotypes. In labial and lingual views, the distal margins of the crowns of V5788, V5790, V5799 (Fig. 8B), V5810, V5821, V5784 are the most recurved, those of V5782 and V5794 are nearly straight, and those of V5780, V5781, V5783, V5790, V5798, V5808, V5814, V5817, V5818 show an intermediate condition. The incompleteness of the crowns of the specimens V5957 and 5962 renders difficult to see the shape of the distal margin. In all the specimens, however, the mesial margin shows the same typical curvature. In mesial and distal (Fig. 8A) views, the largest part of the crowns is slightly concave toward the lingual side. In the cross sections at the base (Fig. 8B) the labiolingually compression is particularly evident, slightly more pronounced toward the distal half of the crown. The crowns appear partly asymmetrical, with a gently convex labial side and a more inflated but nearly trapezoidal labial side which is also markedly concave near the distal carina. The carinae, where preserved, are present along the whole distal margin and at least, the apical half of the mesial one. In particular, the mesial carina is absent for half crown height in V5798, for one third of the crown height in V5810, from the basal portion in V5818, and only at the basal end of V5788 and 5814. Both the carinae bear serrations (Fig. 8C, D), even if the major part of the denticles is broken or heavily worn down. However, it can be seen that the distal denticles are tall more than twice - and sometimes nearly three times - than the mesial ones. The denticles on the mesial carina are in general slightly smaller in base length than those on distal carina, and gradually decrease in size from the apex of the crown to its base, a feature which is particularly evident in V5808 where the apical mesial denticles are larger twice than the basal ones. The mesial denticles are oriented perpendicularly to the edge of the crown, whereas the distal ones are slightly oriented toward the tip of the tooth crown. In some of the specimens the tips of the denticles are preserved too, and appear slightly pointed toward the apex of the crown. Due to the eroded and pitted enamel surface, in the majority of the specimens it is very difficult to see the blood grooves. Nevertheless, in the cases in which they can be seen, they are well developed, visible with the naked eye, and more inclined toward the base of the crown than the denticles are. The only exception is represented by the specimens V5788 and 5957, in which the blood grooves appear slightly shorter and less inclined. In V5799 the enamel preserves shallow curved impressions with the concavity facing toward the tip of the crown. The specimen V5817 has badly preserved enamel and carinae, so that can be tentatively included in this morphotype mainly for its shape. The specimens V5808 and V5810 are tentatively included in this morphotype, even if they have crowns markedly elongated respect to those of the other specimens. The specimens V5806 and V5957 are heavily eroded and broken in several points (in the former the tip and the base are missing, whereas the latter lacks the basal half of the crown), but can be tentatively referred to this morphotype for the features of their preserved portions. The specimen V5962 strongly resembles V5814, although it has pitted and eroded enamel, and lacks the tip and the base of the crown. Finally, the very bad condition of the specimen V5794 renders difficult to recognize any kind of diagnostic features; nevertheless the shape of the crown allow us to tentatively refer it, with a proper degree of caution, to this morphotype.

Comparisons. Although their superficial resemblance with the teeth of

Saurornitholestes (Currie *et al.*, 1990; Brinkman, 2004), the specimens belonging to the morphotype 2 are more labiolingually compressed, have a more curved mesial margin, and have also denticles more pointed and not oriented perpendicularly to the edge of the crown. For the same aspects, the morphotype 2 differs also from the velociraptorine tooth described by Rauhut & Werner (1995) which have shorter denticles and blood grooves not visible. Well visible blood grooves are present in carcharodontosaurids, but they are shorter and less inclined toward the base of the crown (pers. obs. on the teeth of *Carcharodontosaurus saharicus* in the Milano collection labelled MSNM V1479, V2997, V3101) than the blood grooves in this morphotype. Moreover, the teeth of carcharodontosaurids differ from the morphotype 2 in being more elongated and having wrinkles on the crown (Sereno *et al.*, 1996; pers. obs.). Another group of theropods with well developed and inclined blood grooves are the tyrannosaurids, which, however, differ from the morphotype 2 in having stouter crowns labiolingually incrassated. Finally, blood grooves similar to those of the morphotypes 1-3 can be seen in the teeth of the abelisaurids. In *Pycnonemosaurus* from the Late Cretaceous of Brazil (Kellner & Campos, 2002) the blood grooves extend onto the surface of the crown and are inclined toward the base of the crown, and the denticles are inclined too. The teeth of the morphotypes 2 and 3 (see below) closely resemble those of *Majungatholus* (Thevenin, 1907; Sampson *et al.*,1998; Fanti, pers com. 2004; pers. obs. on several specimens in the Milano collection) in having short and labiolingually compressed crowns with a characteristic curvature of the mesial margin, denticles tall, and blood grooves long, well visible and oriented toward the base of the crown. Other than being tall, the denticles are very similar to those of *Majungatholus* also in their general shape (Fanti, pers com.. 2004). The DSDI falls within the range for the abelisaurid specimens from the Cretaceous of Madagascar (Fanti, pers. com. 2004) which include also juvenile specimens, and its mean value (1.24) is nearly the same of the mean DSDI value (1.25) reported by Candeiro *et al.* (2004) for some abelisaurid Brazilian teeth. However, the abelisaurid teeth differ from those belonging to the morphotype 2 for some aspects. The denticles per mm of the morphotype 2 are more numerous, even more than twice, than those ones present in teeth of comparable TCH belonging to both *Majungatholus* (Fanti, pers. com. 2004) and *Pycnonemosaurus* (Kellner & Campos, 2002). In both the morphotypes 2 and 3, and above all in the latter, the cross section at the base is not really drop shaped like in the Abelisaurid teeth from the Cretaceous (Candeiro *et al.*, 2004: fig 4C). Another difference concerns the development of the mesial carina, that is always long as the distal in *Majungatholus* (Fanti, pers. com, 2004) whereas vary in extension among the specimens included into the morphotype 2. Actually, among the neoceratosaurs, teeth with different development of the mesial carina have been reported by Rauhut (2004) in the ceratosaurid *Genyodectes* but not yet in abelisaurids. Also, the BCR in the teeth of *Majungatholus* never exceed the value of 2, whereas some of the teeth belonging to this morphotype are clearly more labiolingually compressed, reaching in one specimen the value of 2.39. As reported by Rauhut (2004), similarly flattened teeth have been found only in the ceratosaurids and advanced carcharodontosaurids (Sereno *et al.*, 1996). Different degrees of recurvature of the distal margin might be instead present also in some abelisaurid teeth, as reported by Candeiro *et al.* (2004).

Fig. 8 - Morphotypes 2 (A-E) and 3 (F-J). Specimen MSNM V5799: distal (A) and labial (B) views, close-ups of the distal (C) and mesial (D) denticles, and cross section at the base (E) of the crown. Specimen MSNM V5779: lingual (F) and distal (G) views, close-ups of the distal (H) and mesial (I) denticles, and cross section at the base (J) of the crown. Abbreviations: d, distal carina; li, lingual side. Scale bars equal 5 mm.

Fig. 8 - Morfotipi 2 (A-E) e 3 (F-J). Esemplare MSNM V5799: viste distale (A) e labiale (B), particolari dei denticoli distali (C) e mesiali (D), e sezione trasversa alla base (E) della corona. Esemplare MSNM V5779: viste linguale (F) e distale (G), particolari dei denticoli distali (H) e mesiali (I), e sezione trasversa alla base (J) della corona. Abbreviazioni: d, carena distale; li, lato linguale. Le scale metriche equivalgono a 5 mm.

Morphotype 3 (Fig. 8F-J)

Referred specimens: MSNM V5779 (Fig. 8F-J), V5809.

Description. This morphotype includes two teeth that undoubtedly occupied a lateral position in the jaws. The crown is recurved on the mesial margin, but nearly straight on the distal one (Fig. 8F). In mesial and distal (Fig. 8G) views, the crown appears slightly concave on the lingual side. The BCR is quite high, especially in V5779 in which it reaches a value of 2.20. The cross section at the base (Fig. 8J) resembles that of the morphotype 2 but has the concavities in the proximity of the carinae even more pronounced. The carinae, present along the entire crown length, contact apically and bear serrations (Fig. 8H, I). The mesial denticles are shorter than the distal ones, but nearly equal in base length. The mesial denticles are oriented perpendicularly to the edge of the crown, whereas the distal ones are inclined toward the tip of the tooth crown. The major part of the denticles is broken or heavily eroded, especially those of the mesial carina. Some denticles of the distal carina, however, are well preserved and appear pointed with the point inclined toward the apex of the tooth crown. The enamel of V5779 is pitted and eroded, but it is still possible to see the blood grooves. In both specimens they are visible even without using a microscope or a lens, and well inclined toward the base of the crown.

Discussion. the teeth included into this morphotype closely resemble those pertaining to the morphotype 2. The only remarkable difference is related to the size of the denticles, that in the morphotype 3 are decidedly larger relatively to the TCH, resulting as large as the denticles of the teeth of the morphotype 1 and *Majungatholus atopus* (pers. obs. on MSNM specimens). Moreover, the mesial denticles have a base length nearly identical to that of the distal ones. For this reason the DSDI results 1.00, a value that is lower than the lowermost DSDI reported for the morphotype 2 but, again, is equal to that of the teeth belonging to the morphotype 1 and falls into the range of variability for abelisaurid theropods (Fanti, pers. com. 2004). As mentioned above, other than the great diversity in denticle size and density, the teeth belonging to this morphotype are virtually indistinguishable from those belonging to morphotype 2, so that the affinities of this morphotypes with the other theropod teeth will be not further discussed.

Morphotype 4 (Fig. 9)

Referred specimens: MSNM V5789 (Fig. 9A-E), V5792, V5800, V5812, V5813, V5956.

Description. This morphotype includes six lateral teeth with crowns recurved (Fig. 9A) and quite labiolingually compressed (BCR approaching but never exceeding the value of 2). In distal view the crown is nearly straight in V5789 (Fig. 9B), whereas it is slightly recurved lingually in the other specimens. The distinctive trait of the teeth included into this morphotype is the cross section at the base (Fig. 9E), which appears drop-shaped (mesially rounded and distally V–shaped) but not completely symmetrical in respect to the mesodistal axis, being the labial side more flattened than the inflated lingual one. Both the carinae, serrated, are well preserved, with the exception of the apical portion of the mesial carina of V5792 that is worn away. They reach the base of the crown in all the specimens, with the exception of V5812 in which the mesial carina is present only for half tooth crown height. The distal denticles (Fig. 9C) are taller and larger than the mesial ones (Fig. 9D) (mean DSDI = 1.44) and are also slightly inclined toward the apex of the crown. They are relatively straight and narrow, and their tips, where preserved, appear almost axe-like or only faintly hooked apically. The mesial denticles are perpendicular to the curved edge of the mesial carina and slightly decrease in size toward the base of the carina. Their tips, where preserved, appear almost squared. The blood grooves are very short and faintly visible. Three of the specimens are not well preserved: V5800 lacks both the apex and the base of the crown, and also its denticles are broken and eroded; V5813 lacks the basal third of the crown; in V5956 only the apical half of the crown is preserved. Finally, the specimen V5812 is tentatively included in this morphotype for its cross section as well as denticle features although in lateral view it resembles much the teeth belonging to the morphotype 6 that are, however, considerably smaller.

Comparisons. Among the eight morphotypes, the denticles of the morphotype 4 recall in some aspects those of the morphotypes 1-3. The mesial denticles are, however, considerably smaller than those of morphotypes 1 and 3, whereas both mesials and distals are relatively larger than those of the morphotype 2. Although partly eroded, the tips of the distal denticles seem less pointed than those of the morphotypes 1-3, and appear more similar to those of *Saurornitholestes* (Brinkman, 2004: 109; pers. obs. on the teeth of *Saurornitholestes* labelled MSNM V5953, V5954, V5955, and housed in the Milano collection) and the velociraptorine teeth described by Sweetman (2004). The blood grooves are nearly equal in shape and development to those of *Saurornitholestes*, and some teeth of this taxon (Sankey *et al.*, 2002) resemble the morphotype 4 also in cross section at the base. The distal denticles of *Saurornitholestes* slightly differ from the ones of the morphotype 4 in being oriented perpendicular to the edge, and the crowns of the latter are not strongly recurved distally like those of the former (Currie *et al.*, 1990; pers. obs.). The velociraptorine teeth figured by Sweetman (2004: fig. 3) are instead comparable with the morphotype 4 in both orientation of the distal denticles and distal curvature of the crowns. The mean DSDI value is higher than those reported for the largest part of theropods (Rauhut & Werner, 1995), with the exception of some forms that have similar (morphotype 6, *Dilong* [Xu *et al.*, 2004], *Richardoestesia* [Rauhut & Werner, 1995], *Saurornitholestes* [Rauhut & Werner, 1995], *Velociraptor* [Rauhut & Werner, 1995], juvenile tyrannosaurids [Currie & Dong, 2001; Carr & Williamson, 2004]) or higher values (*Deinonychus* [Rauhut & Werner, 1995]). The teeth of the morphotype 4 have also denticles with slits wider than those of the velociraptorine teeth described by Rauhut & Werner (1995), but nearly equal in size to the slits of the ones described by Sweetman (2004). Another comparison can be made with some teeth described by Fiorillo & Currie (1994) belonging to a primitive allosaur-like theropod (named "theropod A") from the Upper Cretaceous of Montana. In lateral view, one of them (Fiorillo & Currie, 1994: specimen ANSP 15962, fig. 3d; TCH about 14 mm) resembles very much V5789 in the shape of the crown and denticles; it differs from the morphotype 4 in having denticles with labiolingual axis longer than apicobasal axis, a lower DSDI (about 1), and denticles that clearly end rather than grade into the tooth body. The comparison can be extended also to the teeth belonging to the basal theropods such as coelophysoids or dilophosaur-like forms. Indeed, some Belgian specimens (Godefroit & Knoll, 2003: fig. 6B) from the Late Triassic tentatively referred to the coelophysoid *Liliensternus* have mesial serrations that are slightly smaller than the distal ones, and relatively spaced denticles that are similar in outline to those of the morphotype 4. However, the Belgian teeth differ from MSNM V5789 in having more fine serrations (around 5 per mm on the distal carina), all the serrations perpendicular to the carina, a mesial carina serrated only along the apical two thirds of its edge, and the enamel gently wrinkled on both sides of the crown. The ceratosaur tooth figured by Bakker (2000: fig. 8) closely resembles V5789 in cross section, but appears more elongated in lateral view. However, there are other maxillary teeth of *Ceratosaurus* (Madsen & Welles, 2000: plate I and tooth 8 in plate X) that resemble V5789 also in lateral view. Judging by the photos, the main difference between those teeth and the ones belonging to the morphotype 4 is that in the formers the carinae seem to be well separated from the crown, whereas in the latter they grade into the tooth body. This fact is confirmed by Rauhut (2004) who reported that both the ceratosaurid *Genyodectes* and at least some abelisaurids possess teeth with a flat or even slightly concave area adjacent to the marginal carinae. Finally, the teeth of the ceratosaurids (Rauhut, 2004) do not resemble very much the morphotype 4 in being more labiolingually compressed and in both shape of the crown and DSDI (they have approximately 12 denticles per 5 mm both mesially and distally), but they show also some similar features such as denticles perpendicular to the long axis of the carina, and blood grooves not visible. The last comparison have been made with an Abelisaurid tooth (UFRJ-DG 371-Rd) figured by Candeiro *et al.* (2004: fig. 4C). That specimen closely resembles V5789 in lateral view, both having the distal edge of the crown straight, and the mesial one convex, and in the drop-shaped cross section at the base. The abelisaurid teeth from the Late Cretaceous (Candeiro *et al.*, 2004; Fanti, pers. com. 2004; pers. obs), however, differ from those of the morphotype 4 in having larger denticles pointed apically, lower DSDI (never reaching 1.50), and, as mentioned above, blood grooves long and inclined toward the base of the crown.

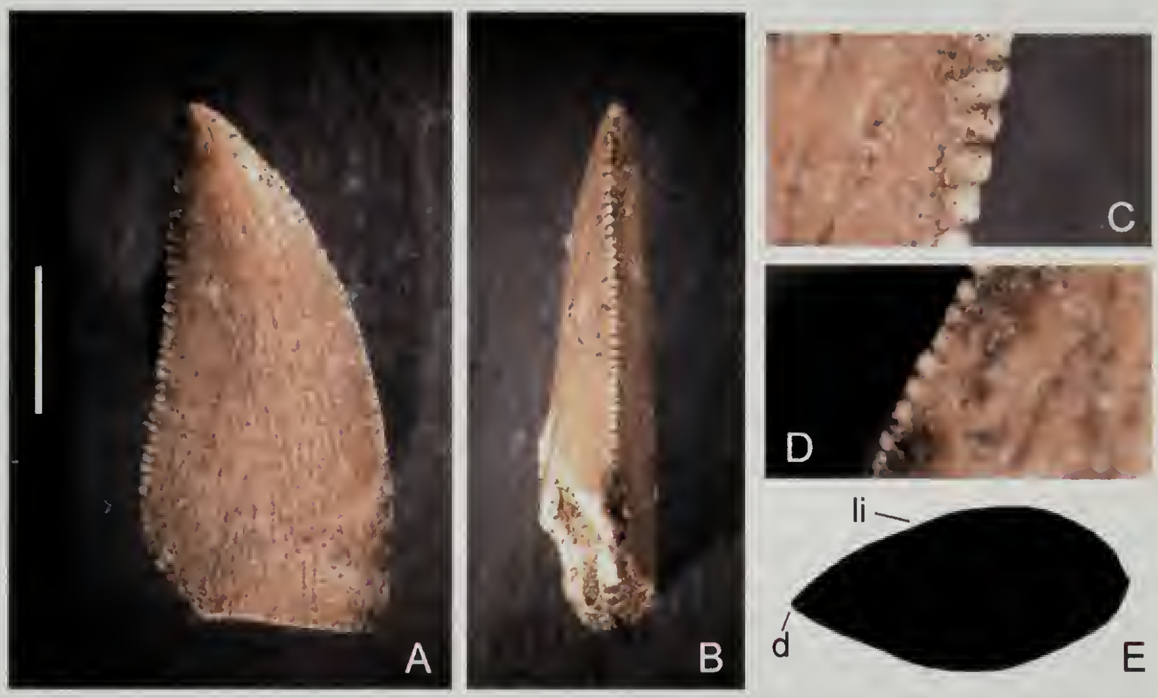

Fig. 9 - Morphotype 4. Specimen MSNM V5789: labial (A) and distal (B) views, close-ups of the distal (C) and mesial (D) denticles, and cross sections at the base (E) of the crown. Abbreviations: d, distal carina; li, lingual side. Scale bar equals 5 mm.
Fig. 9 - Morfotipo 4. Esemplare MSNM V5789: viste labiale (A) e distale (B), particolari dei denticoli distali (C) e mesiali (D), e sezione trasversa alla base (E) della corona. Abbreviazioni: d, carena distale; li, lato linguale. La scala metrica equivale 5 mm.

Morphotype 5 (Fig. 10A-E)

Referred specimens: MSNM V 5791, V5793 (Fig. 10A-E), V5822, V5823, V5824.

Description. The teeth belonging to this morphotype have elongated, faintly bent lingually or nearly straight crowns (Fig. 10A, B). They BCR (mean value = 1.26) is very low, especially in the specimen V5822 (1.04) that is nearly circular in cross section at the base. In cross sections (Fig. 10D, E), the margin of the crown are almost rounded with the exception of the portion of the lingual side near the distal carina, that is markedly flat or slightly concave. The mesial carina is absent, at least in some of the specimens. Indeed, nothing can be said about the mesial carina of the specimen V5791, because all the mesial surface is eroded, while a line of circles along the mesial margin of MSNM V5793 is present that is reminiscent of the bases of very faintly denticles. In distal view, the distal carina, serrated, is not perfectly straight (Fig. 10A): a short apical portion forms a faint concavity turned toward the labial side of the crown, whereas its prosecution, tall as 3/4 of the height of the carina, is faintly concave toward the lingual side. The distal denticles are tall and oriented perpendicularly to the edge of the crown. They are well preserved in V5793 (Fig. 10C) and V5824, in which they appear nearly rectangular with slightly rounded tips (i.e. chisel-shaped). With the exception of V5822, on the mesial portion of the lingual side of the crown the enamel preserves some vertical ridges (Fig. 10B). In V5822 the enamel preserves some wave-like impressions directed mesodistally that are parallel to each other and have the concavity turned toward the apex of the tooth. The distal portion of the lingual side of the crown is smooth and flat, almost depressed near the carina (as can be seen also in cross sections [Fig. 10D, E]). The blood grooves are short, not well marked and perpendicular to the edge of the crown.

Comparisons. The teeth belonging to the morphotype 5 closely resemble those of the morphotype 6. The main differences regard the development of the mesial carina and the BCR, and are verisimilarly linked to a different position in the tooth row. This can be seen at different degrees also in several theropods such as coelophysoids (Colbert, 1989; Rowe, 1989), ceratosaurids (Rauhut, 2004), noasaurids (Carrano *et al*., 2002), compsognathids (Stromer, 1934; Zinke, 1998), and advanced maniraptorans (Xu & Wu, 2001). For this reason we consider the morphotypes 5 and 6 as belonging to the same taxon, with the teeth of the former that would occupy a more rostral position in the jaws than those of the latter. Finally, teeth with vertical ridges on the crown were reported also by Currie *et al*. (1990). Those *"Paronychodon"* - like teeth, however, are different from the teeth belonging to the morphotype 5 for both the development of the ridges and the shape of the crown, which is flattened and ridged on one side, and convex on the other. Vertical ridges on the crown of very similar teeth are present in some specimens figured by Sankey *et al*. (2002: fig. 4) and Brinkman (2004:123) tentatively referred to ?*Dromaeosaurus* sp. Other features of both the denticles and the crown will be discussed below.

Morphotype 6 (Fig. 10F-J)

Referred specimens: MSNM V5786, V5787 (Fig. 10J), V5795 (Fig. 10F-I), V5796, V5797, V5811, V5815, V5816, V5958, V5959.

Description. This morphotype includes ?lateral teeth with crowns elongated, slightly bent lingually (Fig. 10F), and not much labiolingually compressed (mean value of the BCR =1.64). In lingual (Fig. 10G) and labial views, the mesial margin of the crown is gently curved, whereas the distal margin is nearly straight. In two of the specimens (5796, V5797), however, the distal, basalmost portion of both the crown and the distal carina are slightly inclined mesially, then becomes straight as in the other specimens. In cross section at the base (Fig. 10I), the crown is sub-oval;

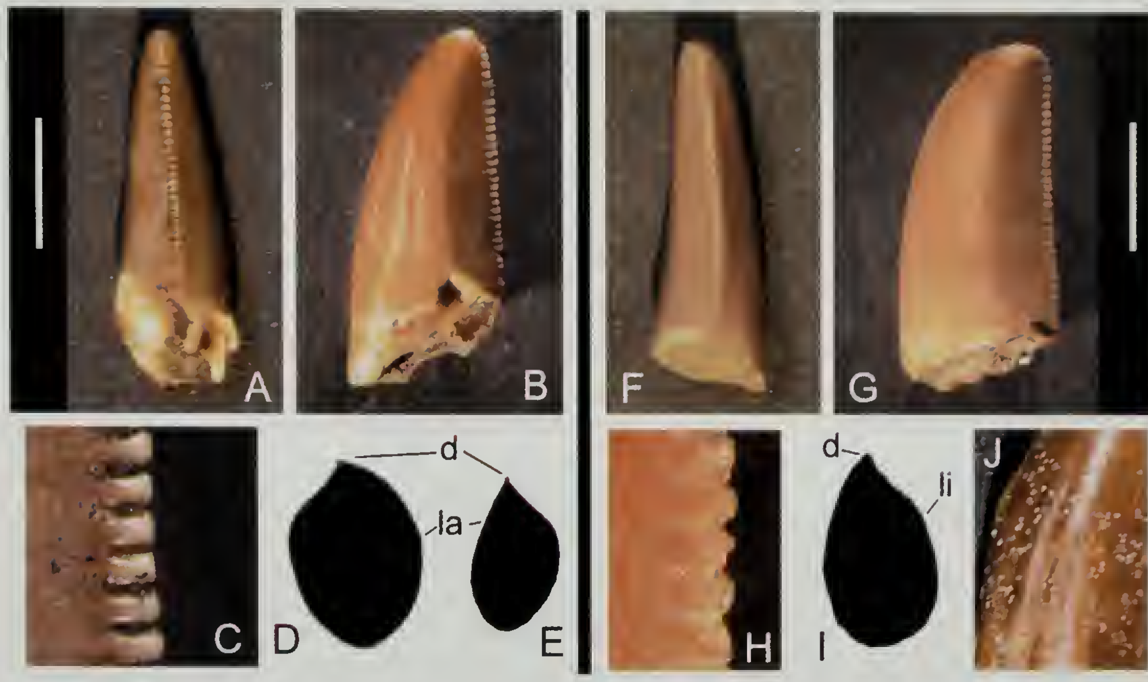

Fig. 10 - Morphotypes 5 (A-E) and 6 (F-J). Specimen MSNM V5793: distal (A) and lingual (B) views, close-up of the distal (C) denticles, and cross sections at the base (D) and mid height (E) of the crown. Specimen MSNM V5795: distal (F) and lingual (G) views, close-up of the distal (H) denticles, and cross section at the base (I) of the crown. Specimen MSNM V5787: close-up of the lingual surface (J) of the crown. Abbreviations: d, distal carina; la, labial side; li, lingual side. Scale bars equal 5 mm.
Fig. 10 - Morfotipi 5 (A-E) e 6 (F-J). Esemplare MSNM V5793: viste distale (A) e linguale (B), particolare dei denticoli distali (C) e sezioni trasverse alla base (D) e a metà altezza (E) della corona. Esemplare MSNM V5795: viste distale (F) e linguale (G), particolare dei denticoli distali (H), e sezione trasversa alla base (I) della corona. Esemplare MSNM V5787: particolare della superficie linguale (J) della corona. Abbreviazioni: d, carena distale; la, lato labiale; li, lato linguale. Le scale metriche equivalgono a 5 mm.

only the labial and lingual margins in the proximity of the distal carina are respectively more flattened and nearly concave. The mesial carina is not preserved in both V5786 and V5797. In the other specimens the mesial carina, never present for more than the apical 3/5 of the tooth crown, develops along the midline of the tooth and bears small serrations that becomes even smaller toward the base of the crown. The distal carina, serrated, is present all along the height of the crown. The distal denticles (Fig. 10H) are tall more than twice than the mesial ones, and are also decidedly larger (mean value of the DSDI = 1.51). The distal denticles are chisel-shaped, whereas the mesial ones have tips nearly squared. All the denticles are oriented perpendicularly to the edge of the crown (heavily eroded till their base in V5787) and the slits that separate each denticle from the others are relatively wide. The blood grooves are shallow, short, poorly defined and perpendicular to the edge. A small portion of the root is preserved in the specimen V5795. On the mesial half of the crown of the specimen V5787 the enamel preserves lingually 2 vertical ridges (Fig. 10J). In V5786 the enamel preserves some wave-like impressions directed mesodistally that have the concavity turned toward the apex of the tooth and are parallel to each other. The crown of the specimen V5959 is slightly more pointed and slender than that of the other specimens, but this kind of differences fall without doubt in the range of the intraspecific variability. Finally, the specimen V5786 is tentatively referred to this morphotype although it is more recurved distally and slightly different in cross section.

Comparisons. The teeth belonging to this morphotype closely resemble the maxillary and dentary teeth of *Dromaeosaurus* (Sankey *et al.*, 2002: fig.4; Brinkman, 2004: 107) in denticle morphology and crown shape and sections, but lacks the more dignostic feature of dromaeosaur teeth, i.e. a mesial carina that is close to the midline of the tooth only apically, then twisting toward the lingual side of the crown. However, also teeth similar to those of *Dromaeosaurus* and having a straight mesial carina were mentioned by Currie *et al.* (1990), who regarded them as a possible new species of dromaeosaurid or a gracile, small form of tyrannosaurid. The teeth of the morphotypes 5 and 6 are also less labiolingually compressed than the dromaeosaurine maxillary and dentary ones, which have a FABL that is much as double the width (Currie *et al.*, 1990). Moreover, in the Dromaeosaurinae the denticles are smallest at both the extremity of the carinae (Currie *et al.*, 1990). The same is true for the mesial carina of the morphotype 6, whereas the distal denticles in morphotypes 5 and 6 decrease in size only toward the apex of the crown. Finally, the blood grooves of *Dromaeosaurus* are very like those of morphotypes 5 and 6, but are usually found only near the base of the tooth (Currie *et al.*, 1990). Denticles with a morphology similar to that of the denticles of the morphotype 5 and 6 can be seen also in some basal tetanurans (Rauhut, 2005a), but the crowns are decidedly different. The mean value of the DSDI of the teeth of the morphotype 6 (1.53) falls within the range for the velociraptorine teeth (Ruhut & Werner, 1995), resulting higher than that of the majority of the theropods. However, it is comparable also with the DSDI reported for other theropod teeth, such as those belonging to the morphotype 4, *Dilong* (Xu *et al.*, 2004), *Richardoestesia* (Rauhut & Werner, 1995), and juvenile tyrannosaurids [Currie & Dong, 2001; Carr & Williamson, 2004]).

Morphotype 7 (Fig. 11A-E)

Referred specimen: MSNM V5785 (Fig. 11A-E).

Description. This morphotype includes only one slender tooth that has the lowermost ER (0.37) among these Malagasy specimens. The crown is moderately labiolingually compressed and nearly straight in mesial (Fig. 11B) and distal views. In cross sections (Fig. 11D, E) the crown is almost suboval, becoming pointed only in correspondence of the distal carina. In labial and lingual (Fig. 11A) views appears well recurved and has a transitional point in which the curvature of the mesial margin becomes more pronounced. The carinae are present on both the mesial and the distal margins, but the mesial one does not extend up to the base of the crown. Both the carinae bear serrations, but are partly worn away, especially the mesial carina in which many denticles are eroded up to their basis. The distal denticles are considerably larger than the mesial ones. All the denticles (see the distal ones in Fig. 11C) are quite short, smaller than in any other Malagasy specimen, simple in form, with faintly rounded tips, and oriented perpendicularly to the edge of the crown. Like some specimens belonging to the other morphotypes, the enamel preserves some wave-like impressions directed mesodistally that are parallel to each other and have the concavity turned toward the apex of the tooth. The blood grooves are hardly visible, and a little portion of the root is preserved.

Comparisons. This tooth closely resembles in all views the tooth figured by Brinkman (2004: 115, fig. 1) and referred to *Richardoestesia isosceles* from the Upper Cretaceous of North America. Being small and relatively simple in form, also the denticles appear quite similar to *Richardoestesia isosceles*, even if a precise comparison can not be made because of the poor preservation of the denticles in MSNM V5785. The same resemblances can be seen in comparing the specimen V5785 with the Spanish teeth referred to cf. *Richardoestesia sp.* (Rauhut, 2002). Another similar tooth (TMP 83.45.2), which is elongated, fang-like, and with an high DSDI, was described and figured by Currie *et al.* (1990, fig. 8.4J) and referred to *Richardoestesia gilmorei*. Additionally, some Portuguese teeth referred to cf. *Richardoestesia sp.* (Zinke, 1998: fig. 6) resemble those of V5785 in denticle size and shape, but clearly differ in having lower DSDIs (range = 0.8 –1.33) and crown that are less recurved and more labiolingually compressed. The morphotype 7 slightly resembles also some teeth of *Nuthetes* (Milner, 2002), the crowns of which, however, are considerably more recurved than those of V5785. Other teeth similar in shape and denticle proportion are those of *Sinornithosaurus* (Xu & Wu, 2001) and *Coelophysis* (Colbert, 1989: fig. 46), but both have finer serrations (more than 8 per mm on the distal carina). Additionally, the teeth of *Coelophysis* have a considerably lower DSDI (0.9-1.2) than V5785, but are quite similar in cross section as can be seen in the tooth of *Coelophysis* housed in the Milano collection and labelled MSNM V5950. The teeth of another coelophysid (Rowe, 1989: fig. 1ABCD) resembles even more V5785 in having among the other features also a transition point, in which the curvature becomes more pronounced, visible along the mesial carina. The same shape of the crown and the transitional point are visible also in some dromaeosaurine dentary teeth (Currie *et al.* 1990), which have, however, denticles different in both size and shape. Also two Belgian specimens (Godefroit & Knoll, 2003) from the Late Triassic show a lanceolate shape similar to that of MSNM V5785, but the Belgian teeth have smaller distal serrations and well-developed but unserrated mesial carinae. The teeth of the holotype of *Dilophosaurus* (Dal Sasso, pers com. 2004) are similar in having slender crowns and denticles simple in form and oriented perpendicularly to the edge; unfortunately, we lack information about the cross section at the base and the denticles of the mesial carina. Finally, the morphotype 7 shows some resemblance with the ceratosaur tooth figured by Bakker (2000), but is considerably less labiolingually compressed than any other ceratosaurid tooth.

Morphotype 8 (Fig. 11F-J)

Referred specimen: MSNM V5819 (Fig. 11F-J), V5961.

The specimen V5961 consists of the distal half of a tooth crown lacking both the apex and the base. It has been included into this morphotype for the morphology of both the denticles and the preserved portion of the crown. The specimen V5819 is the largest well preserved tooth among these Malagasy specimens. The crown is stout, not very much labiolingually compressed (see cross sections in Fig. 11I, J) neither too much elongated. It is also well recurved in labial (Fig. 11F) and

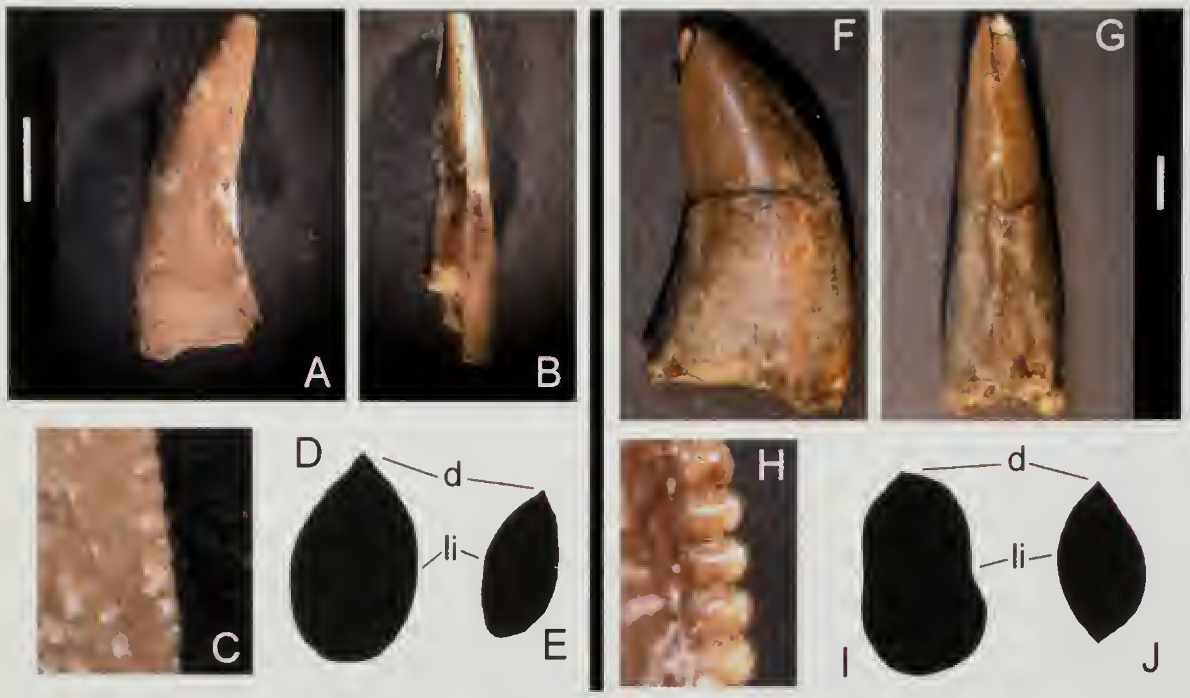

Fig. 11 - Morphotypes 7 (A-E) and 8 (F-J). Specimen MSNM V5785: lingual (A) and mesial (B) views, close-up of the distal (C) denticles, and cross sections at the base (D) and mid height (E) of the crown. Specimen MSNM V5819: labial (F) and distal (G) views, close-up of the distal (H) denticles, and cross sections at the base (I) and mid height (J) of the crown. Abbreviations: d, distal carina; li, lingual side. Scale bars equal 5 mm.

Fig. 11 - Morfotipi 7 (A-E) e 8 (F-J). Esemplare MSNM V5785: viste linguale (A) e mesiale (B), particolare dei denticoli distali (C), e sezioni trasverse alla base (D) e a metà altezza (E) della corona. Esemplare MSNM V5819: viste labiale (F) e distale (G), particolare dei denticoli distali (H), e sezioni trasverse alla base (I) e a metà altezza (J) della corona. Abbreviazioni: d, carena distale; li, lato linguale. Le scale metriche equivalgono a 5 mm.

lingual views, and almost straight in mesial and distal (Fig. 11G) views. Apically, the mesial portion of the crown shows a wear facet that renders impossible to understand if the mesial carina is not preserved or absent. The mesial carina is instead undoubtedly absent on the basal half of the crown. The distal denticles (Fig. 11H) are small and numerous relatively to the TCH. Where preserved, they appear relatively stout, well spaced, chisel-shaped, wider than longer, and oriented perpendicular to the edge of the crown. The size of the denticles slightly decrease toward the base of the crown. The enamel does not show wrinkles, and the blood grooves are short, faintly visible and perpendicular to the edge of the tooth.

Comparisons. The specimen MSNM V5819 resembles somehow the tyrannosaurid tooth from the Dinosaur Provincial Park figured by Brinkman (2004: 129), although the former is slightly narrower labiolingually and more slender than the latter. The denticles are similar in being chisel shape and wider than longer, a feature common in tyrannosaurid teeth (Currie *et al.*, 1990; pers. obs. on the tyrannosaurid teeth in the Milano collection labelled MSNM V5951, V5952). However, in the DPP tooth (Brinkman, 2004) and in other tyrannosaurid teeth (Currie *et al.*, 1990) the slits between the denticles are wider and more lenticular than in MSNM V5819, and the denticles possess sharp ridges of enamel along the midline (maybe worn away in V5819). The blood grooves in tyrannosaurids are well visible and oriented toward the base of the tooth (Currie *et al.*, 1990) but Zinke (1998) reported basal tyrannosauroid teeth (*Aviatyrannis*) from Portugal that differ from the typical tyrannosaurids teeth in having blood grooves not oriented toward the base but perpendicular to the edge as well as in V5819. The number of denticles per mm is also slightly higher than that reported for tyrannosaurids (Farlow *et al.*, 1991) but not too high in considering the tyrannosauroids. In labial and lingual view, both the recurvature of the crown, and the gently wrinkled enamel of the megalosaur tooth figured by Bakker (2000) are reminiscent of those of the specimen V5819. That megalosaurid tooth is, however, more compressed labiolingually and different in cross section (narrower mesially and more symmetric respect to the mesodistal axis). Moreover, in megalosaurids the tooth crowns are usually more elongated than those of the morphotype 8 (Britt, 1991), and have a lower number of denticles per mm (Rauhut & Werner, 1995; pers. obs. 2005). Besides tyrannosaurids, also the allosaurids have tooth crowns thicker labiolingually for their height than are ceratosaurid and megalosaurid crowns, but their serrated carinae are twisted with the posterior carina passing outward from the crown tip and the anterior one passing inward. Again, the shape of the denticles resembles a little more tyrannosaurid theropods than allosaurids (Farlow *et al.*, 1991: fig. 14L,M; pers. obs on the allosaur teeth in the Milano collection labelled MSNM V435, and V5949). Finally, the allosaur teeth (Madsen, 1976) are usually more elongated than V5819, and have a curvature that is usually pronounced only in the apical portion of the crown.

Discussion. It has been proven (Currie *et al.*, 1990) that teeth remains may have great systematic significance in localities which have yielded peculiar morphotypes, above all the ones for which associated cranial or postcranial remains are known too. In studying the systematic and paleobiogeographic significance of theropod teeth from new or poorly known dinosaur localities in which teeth constitute the only remains, however, we have to take into account that tooth morphology greatly reflects functional aspects and for this reason resemblances among the teeth could be related, at least in some cases, to homoplasy. This is particularly true when, due to the poorness of the coeval fossil record, the material may be compared only with specimens that come from fossil sites very distant in space and time. Additional difficulties in teeth identification are partly due to the lack of detailed descriptions and figures for the teeth of several representative taxa for which, on the contrary, cranial and postcranial anatomy is well known. A more complete database including a large amount of information (tooth shape, cross sections, position and development of the carinae, denticles morphology, enamel structures, measurements) and compiled taking into account also ontogenetic, individual, and intraspecific variability would probably increase the systematic value of theropod teeth, and render easier the effort to recognize taxa and test paleobiogeographic hypotheses on the basis of isolated remains. For all these reasons, even if potential affinities have been discussed into the text, at present all the new Malagasy teeth here described must be referred to Theropoda incertae sedis. Nevertheless, the results of the comparisons made in the present study showing some possible affinities with lower-ranked taxa are the following:
- affinities with *Nuthetes* (Milner, 2002), basal tetanurans such as *Condorraptor* (Rauhut, 2005a), and known members of Noasauridae, Spinosauroidea, Carcharodontosauridae, Compsognathidae, Ornithomimosauria, Oviraptorosauria,

Tab. 3 - Basic measurements of the teeth described in the text. Measurements of tooth crown height (TCH), fore-aft basal length (FABL), and tooth basal width (BW) are in mm. Values in brackets are related to the bad preservation of the crown that allows only partial measurements, or to the bad preservation of the carinae that renders the denticle count not accurate; ? indicates that it is impossible to understand if the denticles are really absent or simply not preserved.
Tab. 3 - Misure principali dei denti descritti nel testo. Le misure dell'altezza della corona (TCH) e dei suoi diametri meso-distale (FABL) e labio-linguale (BW) misurati alla base della corona stessa sono espresse in mm. I valori tra parentesi sono riconducibili al cattivo stato di conservazione della corona, che permette solo misure parziali, o delle carene, che rende non accurato il risultato del conteggio dei denticoli. ? indica che è impossibile stabilire se i denticoli sono realmente assenti o se non sono conservati.

specimen	Tooth crown height (TCH)	Fore-aft basal length (FABL)	Tooth basal width (BW)	Basal compression ratio (FABL/BW)	Elongation ratio (FABL/TCH)	Number of serrations per 3 mm of mesial carina	Number of serrations per 3 mm of distal carina	Denticle size difference index (DSDI)
MSNM V5778	25.2	10.5	7.4	1.42	0.42	7	7	1.00
MSNM V5779	24.4	14.1	6.4	2.20	0.58	6	6	1.00
MSNM V5780	10.2	7.8	3.7	2.11	0.76	?	11	-
MSNM V5781	9.1	6.6	3.6	1.83	0.73	15	12	1.25
MSNM V5782	14.9	10.3	5.5	1.87	0.69	10	10	(1.00)
MSNM V5783	12.3	8.1	4.6	1.76	0.66	?	10	-
MSNM V5784	14.1	9.0	4.4	2.05	0.63	13	13	(1.00)
MSNM V5785	18.2	6.8	4.2	1.62	0.37	25	16	(1.56)
MSNM V5786	16.7	7.8	4.0	1.95	0.47	?	12	-

MSNM V5787	13.7	6.6	4.1	1.61	0.48	16	10	(1.60)
MSNM V5788	11.2	6.2	3.1	2.00	0.55	18	15	1.20
MSNM V5789	17.1	8.6	4.4	1.95	0.50	12	8	1.50
MSNM V5790	8.5	6.2	2.7	2.30	0.73	17	13	1.31
MSNM V5791	(12.2)	6.1	4.4	1.39	-	Unserr.	10	-
MSNM V5792	13.8	7.8	4.1	1.90	0.57	15	9	(1.67)
MSNM V5793	11.0	6.0	4.6	1.30	0.55	?	10	-
MSNM V5794	10.2	5.9	3.5	1.69	0.58	23	21	(1.10)
MSNM V5795	13.0	6.0	4.1	1.46	0.46	18	11	1.64
MSNM V5796	12.1	6.9	3.8	1.82	0.57	17	11	1.55
MSNM V5797	(10.9)	6.9	4.9	1.41	-	?	11	-
MSNM V5798	10.4	6.2	3.1	2.00	0.60	14	12	1.17
MSNM V5799	11.8	8.0	3.4	2.35	0.68	15	11	1.36
MSNM V5800	(21.5)	(15.4)	8.2	-	-	11	8	1.38
MSNM V5806	(9.7)	7.1	4.0	1.78	-	15	10	(1.50)
MSNM V5807	28.0	8.6	6.7	1.28	0.31	7	7	1.00
MSNM V580	20.5	9.8	4.1	2.39	0.48	11	9	1.22
MSNM V580	(17.3)	(9.2)	(5.2)	-	-	7	7	1.00
MSNM V5810	21.6	10.4	4.7	2.21	0.48	12	9	1.33
MSNM V5811	13.6	7.1	3.9	1.82	0.52	15	11	1.36
MSNM V5812	(19.2)	(9.2)	5.6	-	-	?	9	-
MSNM V5813	(13.3)	(8.8)	(4.6)	-	-	13	9	(1.44)
MSNM V5814	16.1	8.9	4.9	1.82	0.55	14	11	1.27
MSNM V5815	12.5	6.9	4.4	1.57	0.55	(15.5)	10	(1.55)
MSNM V5816	12.5	6.8	4.2	1.62	0.54	18	12	(1.50)

MSNM V5817	13.7	7.9	4.4	1.80	0.58	15	11	(1.36)
MSNM V5818	(14.6)	8.4	4.3	1.95	-	13	10	1.30
MSNM V5819	31.5	18.0	11.1	1.62	0.57	?	9	-
MSNM V5820	16.4	8.0	6.5	1.23	0.49	7	7	1.00
MSNM V5821	9.7	6.7	3.6	1.86	0.69	?	14	-
MSNM V5822	9.4	5.0	4.8	1.04	0.53	Unserr.	11	-
MSNM V5823	11.4	5.4	4.2	1.29	0.47	Unserr.	12	-
MSNM V5824	11.9	5.4	4.3	1.26	0.45	Unserr.	12	-
MSNM V5956	(9.6)	(7.0)	(4.1)	-	-	?	9	-
MSNM V5957	(14.0)	(6.2)	(2.7)	-	-	?	12	-
MSNM V5958	11.5	5.6	4.0	1.40	0.49	?	11	-
MSNM V5959	12.5	5.9	3.4	1.74	0.47	18	12	1.50
MSNM V5960	(14.4)	(8.3)	(4.7)	-	-	?	?	-
MSNM V5961	(2.00)	-	-	-	-	-	8	-
MSNM V5962	(19.1)	(11.7)	(6.4)	-	-	?	9	-

Tab. 4 - Variation range and mean value (**in bold**) of some tooth parameters in the eight morphotypes. Data taken from Tab. 3 (uncertain data were not taken into account).
Tab. 4 - Valore medio (**in grassetto**) e intervallo entro cui variano alcuni parametri dei denti appartenenti agli otto morfotipi. I dati sono presi dalla Tab. 3 (i dati incerti non sono stati presi in considerazione).

morphotype	1	2	3	4	5	6	7	8
TCH in mm	16.4 –28.0 **23.2**	8.5 – 21.6 **13.0**	24.4 -	13.8 – 17.1 **15.5**	9.4 – 11.9 **10.9**	11.5 – 16.7 **13.1**	18.2	31.5
BCR	1.23 –1.42 **1.31**	1.76 – 2.39 **1.99**	2.20 -	1.90 –1.95 **1.93**	1.04 – 1.39 **1.26**	1.40 – 1.95 **1.64**	1.62	1.62
ER	0.31 –0.49 **0.41**	0.48 – 0.76 **0.63**	0.58 -	0.50 – 0.57 **0.54**	0.47 – 0.55 **0.50**	0.46 – 0.57 **0.51**	0.37	0.57
serr/3mm mesial	7	11 –18 **14.33**	6-7 **6.50**	11 –12 **11.50**	-	15 – 18 **17**	-	-
serr/3mm distal	7	9 – 15 **11.25**	6-7 **6.50**	8-9 **8.60**	10 –12 **11**	10 – 12 **11.1**	16	8-9 **8.50**
DSDI	1.00	1.17 – 1.36 **1.27**	1.00 **1.00**	1.38 – 1.50 **1.44**	-	1.36 – 1.64 **1.51**	-	-

Therizinosauridae, Alvarezsauridae, and Troodontidae (Currie *et al.*, 1990; Brinkman, 2004) can be dismissed;
- the teeth of the morphotypes 1, 2, and 3 show some affinities with both abelisaurid and ceratosaurid teeth (in particular with the formers), and for this reason could be tentatively referred to the Neoceratosauria, if not to the Abelisauridae;
- the teeth belonging to the morphotype 4 are more problematic, sharing features with several taxa, among which the neoceratosaurs and the velociraptorine-grade dromaeosaurids;
- the teeth of the morphotypes 5 and 6 show coelurosaurian affinities, and among the coelurosaurs they recall in particular the dromaeosaurids;
- the morphotype 7 closely resembles some of the teeth referred to the genus *Richardoestesia*, but shares also many features with the coelophysoids and other basal theropods;
- the morphotype 8 shows some resemblances with the teeth of the Tyrannosauroïdea.

The presence of teeth that show a combination of features of both the ceratosaurids and the advanced abelisaurids, may eventually indicate that some yet unknown basal abelisaurids were already present in southern continents during the Middle Jurassic. If this will turn out to be true, it would support a southern origin of the taxon but, at the same time, weaken the previously suggested hypothesis of a South American origin (Bonaparte, 1996; Candeiro *et al.*, 2004). The teeth that show coelurosarian - and in particular dromaeosaurid - affinities may eventually represent the oldest coelurosaurian material from the Gondwanan continents, predating *Nqwebasaurus* from South Africa (de Klerk *et al.*, 2000) approximately 30 million years and dromaeosaurian-like tooth from Ethiopia (Goodwin *et al.*, 1999) approximately 25 million years. The finding of those teeth suggests that the absence of coelurosaurian clades from Gondwana is more apparent than real, given the extremely poor degree to which Jurassic terrestrial vertebrates are currently characterized. The Malagasy coelurosaurian teeth and other Middle Jurassic dromaeosaurid material from the Chipping Norton Limestone Formation, Hornsleasow Quarry, England (Metcalf *et al.*, 1992; Metcalf & Walker, 1994) and from Russia (Novikof *et al.*, 1998), support the idea that coelurosaurian theropods were widely dispersed throughout the world prior to continental isolation, and strengthen the idea that the evolution of the principal coelurosaurian clades has been completed during Early Jurassic. Finally, the specimen MSNM V5819 could represent the only Gondwanan, and by far the oldest, evidence of another taxon of coelurosaurs, the Tyrannosauroidea. However, taking into consideration the above mentioned difficulties in establishing the real systematic value of theropod teeth and the lacking of associated skeletal material, all these potential affinities, and in particular the hypothetic referral of MSNM V5819 to the tyrannosauroids, remain uncertain. As a consequence, at present also the related paleogeographic and stratigraphic range extensions must be regarded with an appropriate degree of caution.

Conclusions

The present study demonstrates the presence of at least three suprageneric theropod taxa in the Middle Jurassic of Madagascar, providing additional information about one of the more biologically productive Middle Jurassic terrestrial ecosystems in which crocodiles and plesiosaurs teeth, sauropod remains (Lydekker, 1895; Thevenin, 1907; Lavocat, 1955; Besairie, 1972; Bonaparte, 1986; Buffetaut, 2003), pterosaur teeth (Dal Sasso & Pasini, 2003) and tribosphenic mammals (Flynn *et al.*, 1999) were present too. Being limited to isolated teeth and bones, the new remains are here referred to Theropoda incertae sedis. Their potential affinities with the Coelurosauria and Abelisauridae, however, are worth to be mentioned, as they would greatly strengthen the significance of this finding in terms of Middle Jurassic Gondwanan paleobiogeography and paleoecology, as well as to theropod evolution. We think that an extensively sample of the Mahajanga Basin could likely yield a greater variety of vertebrate material, as for example in the above mentioned English Bathonian microvertebrate site (Metcalf *et al.*, 1992; Metcalf & Walker, 1994) in which also ornithischian dinosaurs and lizard-like diapsids were collected. More field research in Gondwanan continents is expected to increase our knowledge on terrestrial vertebrates, and given the scarce remains of terrestrial vertebrates predating Late Jurassic, the Mahajanga Basin represents a unique, promising area in terms of both understanding Middle Jurassic ecosystems, and testing biogeographic and evolutionary hypotheses. Besides this, as pointed out more than once in the text above, we also think that the creation of a complete database including the largest possible amount of information about theropod teeth is strongly needed to render easier their identification and fully understand their systematic value.

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